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FAUNA–MICROFLORA INTERACTIONS

E. A. CURL
Department of Plant Pathology, 139 Funchess Hall, Auburn University, Alabama 36849, USA
J. D. HARPER*
Department of Entomology, Auburn University, Alabama 36849, USA

Complex terrestrial ecosystems are created largely by the interactive processes involving protozoa, nematodes and microarthropods in concert with components of the microflora, all responding to the ambient abiotic environment. The relatively large populations and small body size of the micro- and mesoscopic animals, along with their roles in microbial grazing and in nutrient transformations, qualify them for participation in critical rhizosphere phenomena affecting root growth and plant health. By definition of the rhizosphere (Curl and Truelove, 1986) or ectorhizosphere (*sensu* Lynch, 1982), larger animals such as the macroarthropods are not as likely to be directly influenced by environmental changes occurring along the root–soil interface, since they are more transient and not confined to this specific ecological niche.

While many small soil animals are unspecialized feeders, many are microphagous and dependent to a large extent on microflora food sources. These microbial populations are largely dependent on carbon sources derived from rhizodeposition. Consequently, populations of fungi and bacteria are usually larger in the rhizosphere than distant from roots, and microphagous animals tend to congregate in that region.

The interaction of small soil invertebrates and the microflora in organic matter decomposition and nutrient cycling has been extensively documented (Reichle,

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*Present address: Department of Entomology, Box 7613, North Carolina State University, Raleigh, NC 27695, USA

1977; Stout, 1980; Freckman, 1982; Peterson and Luxton, 1982; Coleman et al., 1983, 1984a, 1984b, 1988; Anderson et al., 1984; Seastedt, 1984). While fungi and bacteria are the primary decomposers, microphagous protozoa, nematodes and microarthropods affect the dynamics of the microflora community and directly or indirectly regulate the decomposition process. At the same time, these microbe-feeding animals influence the quantitative and qualitative nature and the behavior of rhizosphere fungi and bacteria that are known to either promote plant growth and health or incite disease.

In this chapter we consider a neglected and poorly understood topic, namely how the activities of soil invertebrates might influence plant pathogen behavior and plant disease. The general relation of small fauna to plant disease, including inoculum transmission, was discussed by Beute and Benson (1979). Here, we attempt to create a new awareness of certain invertebrate activities which may contribute to disease suppression and enhance crop productivity; some background information on the subject has been provided (Curl, 1988). At the same time, equal awareness must be focused upon animal activities that might favor disease.

1. RHIZOSPHERE FAUNA

Before considering our specific topic of disease-related interactions it may be useful to review briefly the functional groups of small invertebrate animals commonly inhabiting the rhizosphere. For convenience these animal groups are assigned to the arbitrary categories of microfauna (free-living protozoa and nematodes) with body widths of < 100 mm and mesofauna (microarthropods) with body widths of < 1–2 mm (Swift et al., 1979). The macrofauna (< 10–20 mm), though important in organic matter fragmentation and decomposition, are largely inhabitants of surface litter rather than of microniches of the rhizosphere. Thus, the micro- and mesoscopic forms, as they feed upon bacteria and fungi at the root surface, offer the greatest potential for altering certain natural rhizosphere processes affecting plant growth, health, and vigor. Except for plant parasitic nematodes, relatively little study has been directed to fauna populations specifically in the rhizosphere. Indeed, the common definition of rhizosphere (Curl and Truelove, 1986) infers a root-system zone of influence primarily affecting activities of the microflora.

1.1. Protozoa

Free-living members of the Protozoa are represented by flagellates, ciliates and amoebae. Laybourn-Parry (1984) has described the classification and functional biology of various groups of the Protozoa. Together they are the most abundant of the micro- and mesofauna, followed by nematodes and the microarthropods. Precise comparisons of their populations with the microflora or with other small animals is difficult due to great differences in methods of isolation and enumeration. For the purpose of this discussion we are primarily concerned with a few genera of the Amoebida which have been studied for implication in the suppression of plant-pathogenic fungi through mycophagous activities. Naked amoebae, estimated at 2×10^3 to $17 \times 10^5\,g^{-1}$ dry weight of soil, constitute the dominant group of soil protozoa (Heal, 1971; Chakraborty and Old, 1985; Old and Chakraborty, 1986). Protozoa, largely amoebae, in an arable field soil have been estimated at 5 g dry wt m^{-2} (Schnurer et al., 1982). Elliott and Coleman (1977) found that 95% of protozoa in a shortgrass prairie following irrigation were naked amoebae. In field experiments Clarholm (1981) observed that peaks of amoebae quickly followed peaks in numbers and biomass of bacteria immediately after rainfall. Interrelationships of amoebae and bacteria leading to acceleration of nutrient mineralization have been extensively researched and discussed (for example, see Elliott et al., 1979; Clarholm, 1981; Coleman et al., 1983, 1984b, 1988). In a suitable physical environment, populations of soil amoebae are largely determined by the availability of food, this being provided mostly by bacteria and to some extent by fungi and algae (Heal, 1970). Since populations of the microflora are greater in the rhizosphere–rhizoplane than distant from roots, it is reasonable to expect higher populations of microphagous amoebae as well within the zone of root influence.

1.2. Nematodes

Rhizosphere and root-surface influence on plant parasitic nematodes is well known, largely relating to egg-hatching reactions to root exudates and the attraction or congregation of larvae around roots in the region of cell elongation. The many ecological phenomena that influence populations and behavior of plant-parasitic nematodes (Norton, 1978; Maggenti, 1981) and their relation to the rhizosphere (Curl and Truelove, 1986) have been discussed. We are concerned here primarily with free-living forms, particularly those that feed upon fungi. Many species of non-parasitic nematodes are associated with plant roots, feeding superficially on the microflora along the rhizoplane. Population densities of free-living nematodes vary widely with season and different kinds of plant cover; estimates for agroecosystems range from 1×10^4 to $18 \times 10^5\,m^{-2}$ (Stinner and Crossley, 1977, 1982). Hendrix et al. (1986) provided summary estimates showing total numbers and biomass of non-parasitic nematodes in conventional-tillage (3008 m^{-2}/344 mg dry wt m^{-2}) and no-tillage (2437 m^{-2}/252 mg dry wt m^{-2}) agroecosystems. Bacteria-feeding species are abundantly represented in such populations, and mycophagous species of *Aphelenchoides, Aphelenchus, Ditylenchus, Neotylenchus*, and other genera are common (Nicholas, 1984).

These nematodes, like the Protozoa, are significantly involved in organic matter decomposition and mineralization, principally through their grazing activities on the microflora (Wasilewska and Bienkowski, 1985; Elliott et al., 1988). Bacterial-feeding nematodes may significantly stimulate bacterial populations in the rhizosphere and increase nutrient availability and uptake

(Coleman et al., 1984b). It follows that intensified microphagous activity in the rhizosphere, while affecting the mineralization of nutrients, may also directly or indirectly influence the competitive behavior of root-infecting fungi and their microbial antagonists.

1.3. Microarthropods

Like other soil invertebrates, populations of microarthropods vary with season, soil chemical and physical factors, kind of vegetative cover, and food availability. Relative numbers of microarthropods per square meter of soil in a European grassland have been estimated at 120 000 for the Acarina (mites) and 40 000 for Collembola (springtails) (MacFadyen, 1957; Kevan, 1965). In Michigan grasslands (Mallow et al., 1985), mite populations reached 80 000 m^{-2} and collembolan populations 18 000 m^{-2} in July. In conventional agroecosystems, the biomass of mites was estimated to be 118 mg and collembolans 17 mg dry wt m^{-2}; biomass figures for both were somewhat higher in no-tillage systems (Hendrix et al., 1986). Though individual species may deviate from the whole-population trend, numbers of both mites and collembolans are generally much higher (depending on season) in grasslands with dense fibrous root systems than in cultivated lands.

The Cryptostigmata or oribatid mites are predominantly soil-dwelling saprophages which feed upon decomposing litter (macrophytic feeders) or on bacteria, fungi and algae (microphytic feeders). Panphytophages are active in either of these categories. The oribatids have exhibited extremely varied feeding preferences, accepting certain foods and rejecting others; they have been most commonly reared on brewer's yeast and other living fungi, dried mushrooms, chopped lichen, and artificial diets such as dextrose and casein (see Butcher et al. (1971) for more on the bioecology of the Acarina). The soil-dwelling Cryptostigmata are most likely to impact upon other biotic components of the rhizosphere whereas the Mesostigmata, Prostigmata and Astigmata are primarily inhabitants of surface litter, compost and dung. The oribatids can be expected to congregate in niches of the rhizosphere where a preferred food supply is available.

Collembola, the most abundant order of the primitive soil-dwelling Apterygota are, like the Acarina, of major importance in organic matter decomposition and nutrient cycling (Edwards et al., 1970; Anderson and Ineson, 1984; Coleman et al., 1984a). Currently, these predominantly microphagous animals also are being recognized for their interactions with mycorrhizal fungi (Warnock et al., 1982; Finlay, 1985; Shaw, 1985; Cromack et al., 1988; Rabatin and Stinner, 1988) and plant pathogens (Curl et al., 1988). The Arthropleona, with elongate, visibly six-segmented abdomens, are typically soil-dwelling and well represented in agricultural soils to 15 cm depth, often following avenues provided by growing roots. Wiggins et al. (1979) found a direct relationship between increased cotton-root density and populations of *Proisotoma minuta* Tullberg and *Onychiurus encarpatus* Denis; further, these species were consistently more abundant in the rhizosphere than in root-free soil. Other common genera in agricultural, forest and grassland soils are *Tullbergia, Friesea, Folsomia* and *Isotoma*.

Populations of collembolans respond positively to both organic and inorganic fertilization (Edwards and Lofty, 1969; Wiggins et al., 1979), and have been known to create problems in greenhouse experiments by feeding upon pathogen inoculum introduced into non-sterilized high-organic plant-growth media. Certain species of *Onychiurus* have been cited as plant pests in situations of low preferred-food availability in fields of sugar beet (Heijbroek, 1972; Dunning and Baker, 1977; Ulber, 1980; Brown, 1985) and several other crops (Ulber, 1980; Getzin, 1985).

2. RHIZOSPHERE FLORA

The quantitative and qualitative nature of the microflora around roots has, unlike that of the fauna, received an enormous amount of research attention since 1904, when Professor Lorenz Hiltner (Hiltner, 1904) coined the term "rhizosphere". Populations and activities of the rhizosphere microflora (Curl and Truelove, 1986) and their influence on crop productivity (Whipps and Lynch, 1986) have been thoroughly documented. Therefore, it will suffice at this point to look at specific groups of bacteria and fungi which relate prominently to plant health and which may be affected by invertebrate animal activities.

Microbial populations, stimulated by rhizodeposition, are almost invariably higher in the rhizosphere than in root-free soil (Fig. 1). Four groups of organisms,

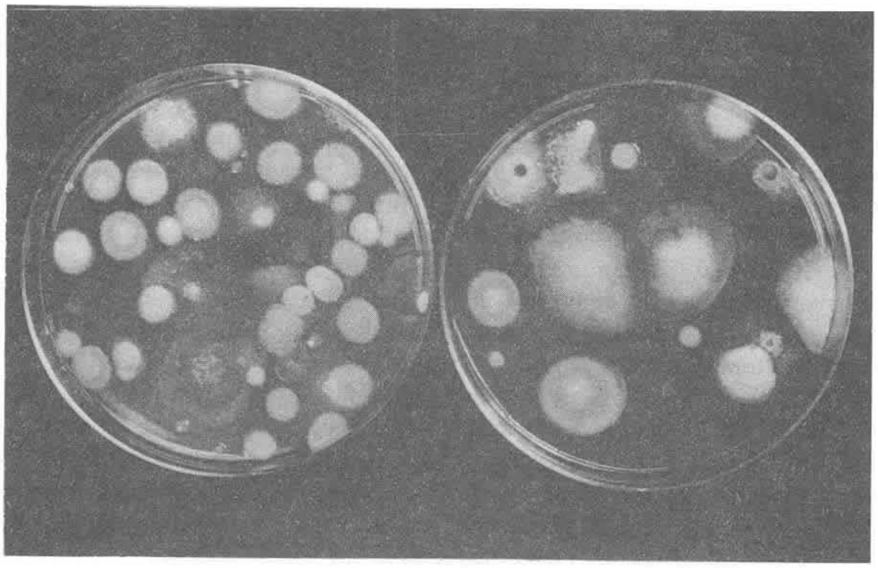

Fig. 1. Dilution plates of fungal colonies from rhizosphere soil (left) and non-rhizosphere soil (right) of wheat, illustrating the greater food potential for mycophagous fauna around roots.

all directly or indirectly related to plant growth and health, are potentially subject to alteration by the activities of microbe-feeding invertebrates. These groups are the plant-growth-promoting rhizobacteria (PGPR), root pathogens, biocontrol organisms and symbiotic organisms.

Populations of bacteria in field soils may exceed 100 million g^{-1} as estimated by soil dilution and plate counts. From such counts the rhizosphere/non-rhizosphere ratio (R/S) values are most frequently in the range 2–20, but ratios over 100 have been recorded. The ratio biomass fungi/biomass bacteria in an arable soil was found to be 5–10 (Shields et al., 1973), and the ratio percent root surface covered by fungi/percent cover by bacteria has been estimated ranging from 0.28 to 14.0 for *Lolium perenne* (Newman et al., 1981). Most prevalent in the rhizosphere are the PGPR (Kloepper et al., 1988), largely composed of *Pseudomonas* spp. Plant growth can be enhanced by *P. fluorescens* and *P. putida* through several mechanisms (Chapter 7).

Soil actinomycetes, predominantly *Streptomyces* spp., are usually second to bacteria in populations, with common R/S ratios of 5 to 10, based on plate counts. Actinomycetes are best known for antibiotic production and the inhibition of plant pathogens and other soil microorganisms. Rouatt et al. (1951) found higher relative numbers of antibacterial actinomycetes in the rhizospheres of several crop plants than in root-free soil.

In general populations of fungi are lower than those of bacteria and actinomycetes, though 100 000 colony-forming units g^{-1} dry wt of soil is not uncommon (Rouatt et al., 1960). The R/S ratios derived from plate counts may range from 3 : 1 to >100 : 1 but most frequently are 10 : 1 to 20 : 1 for crop plants. By the use of selective inhibitors and measurement of CO_2 production, the metabolically active biomass ratio of fungi/bacteria has been found to range from 1.5 to 9 in agricultural, grassland and forest soils, and from 0.13 to 1.5 in rhizospheres of crop plants and prairie grasses (Anderson and Domsch, 1975, 1980; Vancura and Kunc, 1977; Nakas and Klein, 1980). Thus, whereas fungi in bulk soil usually exceed bacteria in biomass, either group in the rhizosphere may have the larger biomass (Newman, 1985). Saprophytic fungi as well as bacteria in the rhizosphere create a competitive deterrent to pathogen colonization of the rhizoplane. Some saprophytes, such as species of *Trichoderma* and *Gliocladium*, produce toxins or become directly parasitic on root pathogens. Other common fungi in the rhizosphere include species of *Penicillium, Aspergillus, Fusarium, Cladosporium, Cephalosporium*, the Mucorales and nematode-trapping Hyphomycetes.

Garrett (1970) categorized root-infecting fungi as either specialized root-inhabiting fungi characterized by a declining or weakly competitive saprophytic phase after death of the host plant, or soil-inhabiting pathogens characterized by a strong competitive ability (expanding saprophytic phase in absence of the host plant). Most highly specialized are the symbiotic fungi represented by ectomycorrhizal species of Basidiomycetes in the genera *Pisolithus, Laccaria, Boletus, Thelephora, Suillus, Amanita, Lactarius, Corticium*, and *Rhizopogon*. Endomycorrhizal species of the Endogonaceae are found in the genera

Gigaspora, Glomus, Acaulospora and *Sclerocystis* (see also Chapter 11). Specialized root pathogens are represented by such common species as *Plasmodiophora brassicae* Woron., *Phymatotrichum omnivorum* (Sheer) Duggar, *Gaeumannomyces graminis* (Sacc.) Arx et Olivier, *Verticillium dahliae* Kleb. and the vascular wilt fusaria. Root-infecting fungi with high competitive saprophytic ability include *Pythium* spp., *Rhizoctonia solani* Kühn, *Aphanomyces euteiches* Drechs., *Fusarium solani* f. sp. *phaseoli* (Burk.) Snyd. et Han., and *Cochliobolus sativus* (Ito et Kuirg.) Drechs. ex Dastur.

These fungi collectively produce a variety of propagules (conidia, chlamydospores, sporangia, zoospores, sclerotia, rhizomorphs) which serve as inocula and/or survival structures. They provide opportunities for mycophagous invertebrate animals to influence pathogen behavior or survival, either in the passive state of the fungus or during root colonization and infection.

3. ROLE OF FAUNA IN PLANT DISEASE SUPPRESSION

Great differences in the natural disease-suppressive capacity of cropped soils have been observed since the early 1900s but the mechanisms involved are not entirely clear (Baker and Cook, 1974; Schneider, 1982; see also Chapter 15). While most efforts to explain the phenomenon relate to microbial antagonisms, soil mycostasis and physico-chemical soil properties, it is essential that we adopt a holistic approach (Lyda, 1982) to such studies, knowing that no single biological phenomenon in the rhizosphere is likely to determine the capacity of a soil-borne pathogen to establish a disease relationship. Invertebrate animals that consume or inactivate pathogen inocula have only recently received serious attention as disease suppressants. Mycophagous amoebae, nematodes and

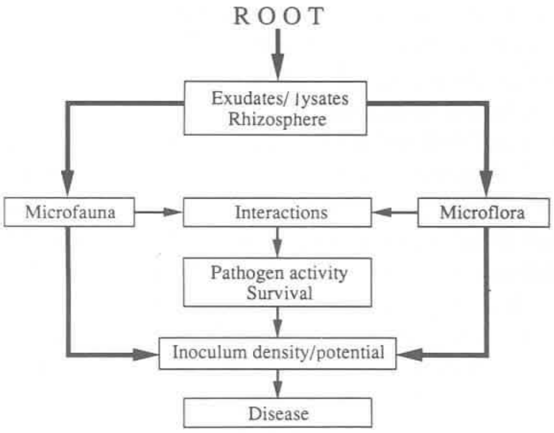

Fig. 2. Schematic representation of rhizosphere influence on the soil microfauna and microflora, ultimately affecting root pathogen activities and disease potential.

microarthropods are the targets of relatively new research in this regard. Fig. 2 shows a schematic representation of the interrelationship of microfauna and flora in the rhizosphere and potential impact on pathogen activities and disease. Biotic relationships are further influenced by the ambient chemical and physical environment around roots.

3.1. Mycophagous Amoebae in the Rhizosphere

High populations of amoebae in plant rhizospheres are reflected in reports of R/S ratios ranging from 2 : 1 for total protozoa to 20 : 1 for specific mycophagous amoebae (Rouatt et al., 1960; Geltzer, 1963; Darbyshire and Greaves, 1967, 1973; Napolitano, 1983; Chakraborty et al., 1985). Old and Chakraborty (1986) have reviewed the biology and significance of mycophagous soil amoebae in relation to suppression of soil-borne plant pathogens and disease. Therefore, it is only necessary here to summarize certain key points and provide update information.

Among the genera of amoebae known to be fungal feeders are *Arachnula, Cashia, Gephyramoeba, Mayorella, Saccamoeba, Thecamoeba, Theratromyxa* and *Vampyrella*. A wide range of fungal species, and in many cases bacteria and algae, serve as food for amoebae; food selectivity or preference is common. Feeding activity results in either perforation lysis, in which cell walls are penetrated, leaving uniform holes 0.2–6.0 μm in diameter, or general lysis, in which fungal propagules taken into digestive vacuoles are ruptured following lysis of the cell wall. Different fungal species have been reported to be resistant to attack by specific amoebae (Esser et al., 1975; Old and Darbyshire, 1978; Chakraborty et al., 1983). However, the great nutritional diversity of amoebae and the ability of certain species to destroy both pigmented and hyaline propagules suggest the improbability that any fungal species is totally resistant.

Recognition that mycophagous amoebae may destroy considerable fungal biomass, particularly in the rhizosphere, prompted serious investigations to determine the potential impact of such activities on inoculum density–disease relationships. Anderson and Patrick (1978) demonstrated that vampyrellid amoebae isolated from field soil in Ontario perforated and fed on chlamydospores and mycelium of *Thielaviopsis basicola* (Berk. et Br.) Ferr. and conidia of *Cochliobolus sativus*, resulting in reduced populations of viable propagules of both fungi. Preliminary greenhouse tests showed that populations of both fungi could be reduced by adding cysts of the amoebae to soil. The amoebae feed on pigmented spores, as well as hyaline propagules, thus suggesting a potential for destroying spores generally believed resistant to many other biotic factors (Old and Patrick, 1979). During this period, the effectiveness of mycophagous amoebae as biological control agents under field conditions was postulated but not tested.

Chakraborty et al. (1983) and Chakraborty (1985) found that the population of viable propagules of *Gaeumannomyces graminis* var. *tritici* Walker (take-all disease pathogen) declined more rapidly in take-all suppressive soil than in non-suppressive soil. Mycophagous amoebae were strongly implicated when higher numbers were found associated with the fungus in suppressive soils than in disease-conducive soils. Subsequently, Chakraborty and Warcup (1985) reported the suppression of *G. graminis* var. *tritici* and take-all disease of wheat in pot bioassays using mycophagous amoebae. *Gephyramoeba* sp., *Saccamoeba* sp. and *Thecamoeba granifera* Greef. subsp. *minor* Pussard, when added to sterilized non-suppressive soil infested with the pathogen, reduced disease severity and increased plant height and shoot dry weight. Mixed populations of the amoeba species also provided significant disease control. Thus, it is possible that inoculum-destroying amoebae may contribute to the natural suppressive-soil phenomenon in wheat fields.

3.2. Nematode–Fungus Relationships

Fungus-feeding nematodes are ubiquitous in soil; many belong to the genera *Aphelenchus, Aphelenchoides, Ditylenchus, Neotylenchus* and *Paraphelenchus* (Nicholas, 1984). Some species are primarily bacterial feeders, omnivores or predators. A wide variety of fungi, both saprophytes and plant pathogens, serve as suitable food sources for mycophagous nematodes, thus suggesting unspecialized feeding habits. Consideration of mycophagous nematodes for biological suppression of fungal pathogens and root diseases has involved primarily species of *Aphelenchus* and *Aphelenchoides*.

Aphelenchus avenae Bastian is commonly found associated with roots, tubers and rhizomes, but most nematologists consider the species to be mycophagous or saprophagous. Mankau and Mankau (1963), in laboratory cultures, demonstrated highly favorable effects of *Rhizoctonia solani, Periconia* sp., *Verticillium alboatrum* (Reinke et Berth.), *Fusarium solani* (Martius) Sacc. and *Thielaviopsis basicola* on reproduction and development of *A. avenae.* Contrastingly, saprophytic soil fungi such as *Aspergillus terreus* Thom, *Penicillium* sp., *Rhizopus nigricans* Ehrenberg and *Trichoderma viride* Pers. ex Fries., were not favorable food sources. Pythiaceous fungi, including plant pathogens *Pythium ultimum* Trow, *Phytophthora parasitica* Dastur., *P. citrophthora* (R. et E. Smith) Leonian and *P. cryptogea* Pethy et Laff., also were poor food bases for *A. avenae* and apparently were toxic. Studies in France (Cayrol and Combettes, 1977) showed that neither *A. avenae* nor *Aphelenchoides composticola* Frank prevented growth of *P. ultimum* in Petri dishes but both were aggressive on cultures of *R. solani.* Townshend (1964) observed that *A. avenae* could feed and reproduce on 54 of 59 fungal species tested. The nematode can readily pierce cell walls of gill tissue in basidiomycetes and ingest the cytoplasm (Walker, 1984).

Aphelenchoides spp. are largely polyphagous, feeding and reproducing on a variety of phytopathogenic fungi. Their populations were predominant around lower stems of barley and wheat in Germany (Rossner and Urland, 1983). Certain species can be reared in large populations on specific fungi, such as *Agaricus campestris* Link ex Fries, for experimental purposes (Rossner and Nagel, 1984).

Effective control of several root-infecting fungi in artificial greenhouse environments has been achieved by using relatively large populations of *A. avenae*. For control of root rot (*Pythium arrhenomanes* Drechs.) of corn, 125 000 nematodes per pot (15 cm diameter) of autoclaved soil were required (Rhoades and Linford, 1959). The nematode only invaded roots that had been invaded by *Pythium* and did not invade healthy roots where *Pythium* was absent. *Aphelenchus avenuae* populations of 100 000 per pot (13 cm diameter) of soil provided excellent control of *Rhizoctonia solani* on bean (Barker, 1964), whereas 10 000 nematodes were relatively ineffective. Barnes et al. (1981) controlled *R. solani* and *Fusarium solani* on alfalfa seedlings by infesting pots of soil with 250 000 to 1 million nematodes. While these large populations would not be expected to occur commonly around roots, such artificial tests do suggest a potential role for mycophagous nematodes in the natural reduction of inoculum density of certain pathogens.

Aphelenchoides cibolensis Riffle and *A. composticola* suppressed the development of *Armillaria mellea* (Vahl. ex Fries) Karst. and root-rot disease of *Pinus ponderosa* Laws in flasks of agar–sand cultures (Riffle, 1973). However, the fungus was not eradicated, suggesting that the nematode may be more effective in preventing development of the fungus initially than in preventing invasion of root tissue after the pathogen becomes established at the rhizoplane. In greenhouse pot trials with *Aphelenchoides hamatus* Thorne et Malek, damage to wheat caused by *Fusarium culmorum* (W. G. Smith) Sacc. was significantly reduced (Rossner and Nagel, 1984). Thus, while extensive field tests have not yet been conducted, the potential role of these relatively abundant pathogens seems evident.

3.3. Role of Microarthropods in Plant Pathogen Suppression

Prominent among the Acarina are non-predatory forms that feed primarily as mycophages and saprophages. The ability of some mite species to feed on higher plants probably evolved from early development of mycophagous habits (Krantz and Lindquist, 1979). In managed agricultural systems, the phytophagous economic pest species have received most attention, while the bulk of literature on the fungus-feeding acarinids has concentrated on their role in organic matter decomposition and nutrient cycling in forest and pasture ecosystems. Whereas the possibility that soil mites may transport pathogen propagules and promote plant disease is recognized (Beute and Benson, 1979), little effort has been made to determine the potential of mycophagous species to suppress pathogen activities. Many of the Cryptostigmata, or oribatid mites, prefer the pigmented fungi (Mitchell and Parkinson, 1976), which otherwise are usually highly resistant to stress conditions in field soil. The capacity of mites to alter the inoculum density of dark pigmented pathogens, such as *Rhizoctonia solani, Thielaviopsis basicola* and *Cochliobolus sativus*, and reduce disease potential is worthy of more investigation.

3.3.1. Collembolan Grazing Activities

Selective grazing pressure by collembolans on the microflora of soil/litter systems and roots could be significant, depending upon the animal populations, growth rate of the grazed organisms, and suitability of the fungi or bacteria as food sources; some produce toxic metabolites (Visser, 1985). We have observed in laboratory feeding tests with *Proisotoma minuta* and *Onychiurus encarpatus*, the most prevalent collembolan species in the cotton rhizosphere in Alabama, that fewer than 100 insects per 30 mm-diameter colony of *Rhizoctonia solani* were unable to totally destroy the pathogen (unpublished data); the rapid growth rate of the fungus partially negated the grazing effect of the animals. A population of 200 insects, however, rapidly consumed a young colony leaving only mycelial aggregations or multiple strands. The effect of grazing on respiration of a fungus also may be linked with the nutrient concentration of the growth medium (Hanlon, 1981). Grazing by *Folsomia candida* Willem. on cultures of the fungus *Botrytis cinerea* Pers. ex Fries, grown on vermiculite granules at low nutrient levels derived from Czapek-Dox solutions, resulted in a significant decline in fungal activity. Conversely, grazing on cultures grown at higher nutrient concentrations stimulated fungal respiration.

While collembolans generally are unspecialized feeders, the capacity of some species to destroy or restrict growth of certain fungi and inflict little damage on others is clearly evident. Mixed populations (200 animals) of *P. minuta* and *O. encarpatus* totally prevented growth from mycelial disks of the soil-borne plant pathogens *R. solani, Macrophomina phaseolina* (Tassi) Goid., *Verticillium dahliae*, and *Fusarium oxysporum* f. sp. *vasinfectum* (Atk.) Snyd. et Hans. on Czapeks agar, but at the same time had little effect on the pathogen *Sclerotium rolfsii* Sacc. or the popular biocontrol agent *Trichoderma harzianum* Rifai (Curl et al., 1985a). In further laboratory tests, Lartey et al. (1989) found that the two collembolan species grazed preferentially on *R. solani* in the presence of *T. harzianum* and two other biocontrol agents, *Gliocladium virens* Miller, Giddens et Foster and *Laetisaria arvalis* Burdsall (Table 1). It was discovered that high mortality rates among the insects occurred on cultures of *T. harzianum* and *G. virens* at the time of fungal sporulation, suggesting either toxic effects of fungal metabolites or direct parasitism of insects by the fungi. Cultures of *L. arvalis* were not lethal to the insects, but egg production was reduced, compared to high egg populations of insects grazing on *R. solani*.

3.3.2. Collembolan Relation to Fungal Propagules

Fungal spores and hyphal fragments, particularly of the dematiaceous hyphomycetes, are commonly found in the gut contents of collembolans (Poole, 1959). This suggests the probability that ingested fungal propagules, perhaps still viable, could be deposited in fecal pellets at the root–soil interface, or that the inoculum density of a root pathogen might be reduced and affect disease incidence.

TABLE 1. Attraction of mycophagous insects to colonies of *R. solani* and three biocontrol fungal agents when the insects were applied to a water agar surface simultaneously with the fungi. From Lartey et al. (1989)

	Number of insects attracted to:		
Fungal agent	*Fungal agent*[a]	*R. solani*[a]	χ^{2b}
	Proisotoma minuta		
G. virens	196	333	17.74***
T. harzianum	67	384	222.81***
L. arvalis	82	307	136.16***
	Onychiurus encarpatus		
G. virens	84	360	171.57***
T. harzianum	81	350	167.89***
L. arvalis	150	340	73.76***

[a] Values represent total counts for eight replications; only insects in contact with a food source were included in the analysis.

[b] *** represents $P < 0.001$.

The collembolans, *P. minuta* and *O. encarpatus*, from the rhizosphere of cotton, were used in a series of laboratory tests to determine feeding effects on pathogen propagules (Curl et al., 1985a). The insects were attracted to washed chlamydospores of the cotton-wilt pathogen, *Fusarium oxysporum* f. sp. *vasinfectum* on a water–agar surface; spores ingested and redeposited in fecal pellets were reduced in germinability. When chlamydospores in water suspension were placed on Millipore membrane filters and buried in either sterilized or nonsterilized sandy loam artificially populated with collembolans (1600 kg^{-1} soil), the spore population after 10 hours was significantly reduced. Germination of chlamydospores that were ingested and redeposited in fecal pellets also was greatly reduced.

The collembolans were not able to infest or destroy mature macrosclerotia of *Sclerotium rolfsii* or the microsclerotia of *Verticillium dahliae* and *Macrophomina phaseolina*, thus they did not reduce sclerotial populations. However, the germination rate of sclerotia in the presence of the insects was significantly reduced (Fig. 3); the highly efficient grazing of germ tubes by the animals essentially rendered the sclerotia ineffective as viable propagules.

3.3.3. Modification of Fungal Populations in the Rhizosphere

Collembolans can alter the quantitative nature of fungi in the rhizosphere (Curl et al., 1983). A mixed population of *P. minuta* and *O. encarpatus* (500/140 g soil) was applied to a natural sandy loam in large glass tubes with cotton seedlings. Six days later, soil dilution and plating procedures revealed a change in the R/S ratio of total colony-forming units of fungi per gram of soil from

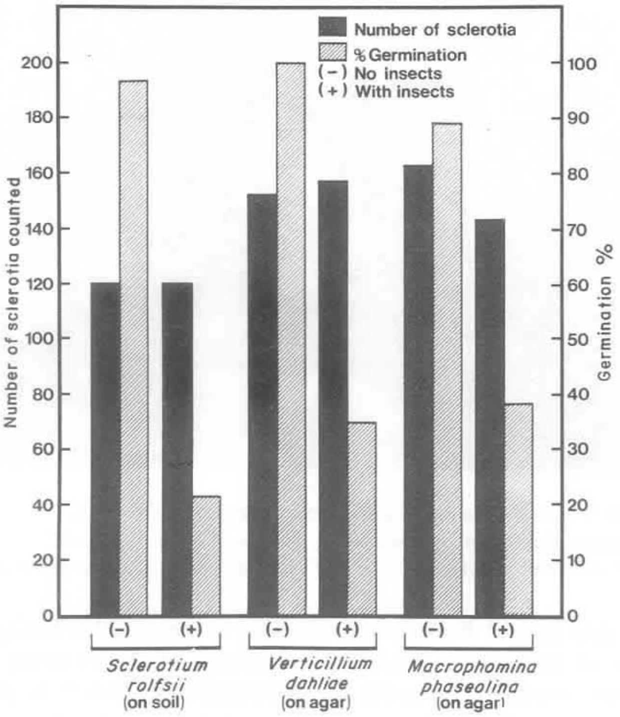

Fig. 3. Effects of collembolans on the sclerotia of three plant pathogenic fungi.

R/S = 2.40 in the absence of insects to R/S = 0.41 in soil with insects. The R_0/R_c ratio (R_0 = no insects, R_c = collembolans present) for rhizosphere soil was 6.94, indicating a significantly lower fungal population in soil with insects present.

Specific tests with *Fusarium oxysporum* f. sp. *vasinfectum* further demonstrated the impact of the collembolan species on inoculum density. Chlamydospores of the pathogen were applied to sterile hypocotyls of pregerminated cotton seed before transplanting to tubes of sterilized soil with or without insect populations. A significant decrease in the viable spore populations of rhizosphere soil had occurred 48 hours after the soil was infested with collembolans. The relation of this activity to the incidence of fusarium wilt in cotton has not been determined.

3.3.4. Biological Control of Root Disease

The capacity of the Collembola to consume relatively large amounts of fungal mycelia and suppress pathogen activities led to further investigations at the

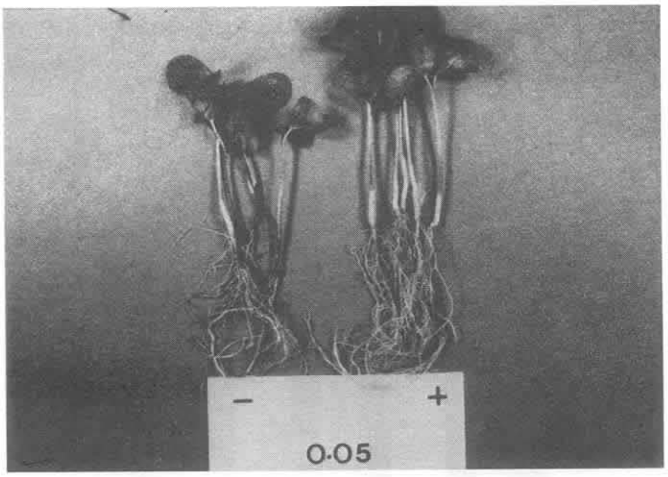

Fig. 4. Control of *Rhizoctonia solani* and cotton seedling disease by mycophagous collembolans (*Proisotoma minuta* and *Onychiurus encarpatus*, mixed populations). (−) = no insects in soil infested with *R. solani* inoculum at 0.1 g kg^{-1}, (+) = 1700 insects kg^{-1} added to pathogen-infested soil.

Alabama Agricultural Experiment Station to assess the biological control capabilities of laboratory reared populations of *Proisotoma minuta* and *Onychiurus encarpatus*. The earliest demonstration of disease suppression (Curl, 1979) was performed with cotton seedlings in large glass tubes (35 mm × 20 cm) of sterilized sandy loam infested with *Rhizoctonia solani* mycelium at 0.05 kg g^{-1} (wet wt) and mixed populations of the two insect species at either 1600 kg^{-1} soil or 4800 kg^{-1}. Surface sterilized cotton seeds were germinated on a nutrient agar and uncontaminated seedlings transplanted to the tubes. Assessment 12 days after planting showed that seedling root disease was significantly reduced by the collembolan populations, the higher number of insects being most effective. Plants in sterilized soil containing only Collembola were stimulated in growth, suggesting that plant-growth-promoting bacteria from the insect gut may have colonized the rhizosphere.

Subsequent greenhouse tests (Curl et al., 1985b) showed that collembolan populations of 1000 to 2000 kg^{-1} soil were about equally effective for disease suppression where the inoculum density of *R. solani* was less than 0.5 g kg^{-1} soil (Fig. 4). Lartey et al. (1986) discovered that disease control was further enhanced when either of the three biocontrol fungi, *T. harzianum, G. virens* or *L. arvalis* was added to soil along with insect populations. These fungal agents are not preferred food for the two collembolan species (Lartey et al., 1989).

4. CONCLUSIONS AND PROJECTED EMPHASIS

The rhizosphere harbors a complex community of interacting microflora and small invertebrate fauna, responding to root exudates, lysates and sloughed root cells, and directly or indirectly affecting the growth and productivity of plants. Protozoa, free-living nematodes, and microarthropods have long been recognized for their role in organic matter decomposition and nutrient cycling, whereas their activities in the rhizosphere relating to root pathogen behavior and survival have received relatively little attention. However, recent investigations have provided strong evidence that certain species of these predominantly mycophagous animals can consume pathogen propagules in sufficient quantity to significantly reduce inoculum density and disease potential, thus effecting a degree of biological control.

This kind of faunal activity suggests the need for a new look at the mechanisms that have been proposed to explain the phenomenon of disease-suppressive versus conducive soils (Schneider, 1982). Where disease-conducive soils, once heavily infested with specific pathogen inocula, gradually become suppressive, the potential contributions of micro- and mesoscopic fauna to this process should be considered along with the popular theory of microbial antagonism (competition and antibiosis). This seems particularly logical in fields subjected to cultural practices (rotations, turning under crop refuse, minimal tillage) which increase the organic matter content of soils, this condition being highly favorable for small fauna activity.

While natural disease suppression by any biotic agent is viewed as highly desirable, it is recognized at the same time that small invertebrates, particularly the microarthropods with bristled bodies and gut contents of ingested microbial components, may transport undesirable organisms from the edaphosphere (non-rhizosphere soil) into the rhizosphere, creating adverse conditions for plant growth. Further, current efforts to genetically transform and manage bacterial and fungal agents for disease control must take into account the small-animal relationship, whether compatible with or adverse to specific biocontrol agents to be established on seeds and roots.

Finally, we know little about the interactions of fungus-feeding microarthropods and other small animals with the ecto- and endomycorrhizal fungi. Few plants in natural ecosystems are without mycorrhizas, and it is now recognized that the rhizodeposition chemistry of roots with the fungal symbionts may create a mycorrhizosphere which determines the composition of the microflora and in turn affects animal species diversity (see Fogel, 1988). Depending upon the food preference of specific animals within an ecological niche, herein lies the potential for mycophagous species to reduce mycorrhizal competition from other fungi or to interfere with establishment of the symbiotic association. The end result could affect not only nutrient cycling but also the incidence of root disease, since the ectomycorrhizal mantle or sheath over young feeder roots is believed to function in a protective capacity (see Schenck, 1981).

A thorough understanding of specific fauna–microflora relationships in the rhizosphere and their consequences to plant health, growth and function could lead to management strategies beneficial to crop production.

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